10-10-2012

Bryophyte species composition over moisture gradients in the Windmill Islands, East Antarctica: development of a baseline for monitoring climate change impacts

J Wasley
University of Wollongong

S A. Robinson
University of Wollongong, sharonr@uow.edu.au

J D. Turnbull
University of Wollongong, jdt17@uow.edu.au

D H. King
University of Wollongong, dhk442@uowmail.edu.au

W Wanek
University of Vienna, jane.wasley@aad.gov.au

See next page for additional authors

Bryophyte species composition over moisture gradients in the Windmill Islands, East Antarctica: development of a baseline for monitoring climate change impacts

Abstract

Extreme environmental conditions prevail on the Antarctic continent and limit plant diversity to cryptogamic communities, dominated by bryophytes and lichens. Even small abiotic shifts, associated with climate change, are likely to have pronounced impacts on these communities that currently exist at their physiological limit of survival. Changes to moisture availability, due to precipitation shifts or alterations to permanent snow reserves, will most likely cause greatest impact. In order to establish a baseline for determining the effect of climate change on continental Antarctic terrestrial communities and to better understand bryophyte species distributions in relation to moisture in a floristically important Antarctic region, this study surveyed finescale bryophyte patterns and turf water and nutrient contents along community gradients in the Windmill Islands, East Antarctica. The survey found that the Antarctic endemic, Schistidium antarctici, dominated the wettest habitats, Bryum pseudotriquetrum distribution spanned the gradient, whilst Ceratodon purpureus and Cephaloziella varians were restricted to the driest habitats. These patterns, along with knowledge of these species relative physiology, suggest the endemic Schistidium antarctici will be negatively impacted under a drying trend. This study provides a model for quantitative finescale analysis of bryophyte distributions in cryptogamic communities and forms an important reference site for monitoring impacts of climate change in Antarctica.

Keywords

over, east, composition, species, islands, bryophyte, windmill, development, baseline, monitoring, climate, gradients, change, impacts, moisture, antarctica

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

Publication Details

Wasley, J., Robinson, S. A., Turnbull, J. D., King, D. H., Wanek, W. & Popp, M. (2012). Bryophyte species composition over moisture gradients in the Windmill Islands, East Antarctica: development of a baseline for monitoring climate change impacts. Biodiversity, 13 (3-4), 257-264.

Authors

J Wasley, S A. Robinson, J D. Turnbull, D H. King, W Wanek, and M Popp

RESEARCH ARTICLE

Bryophyte species composition over moisture gradients in the Windmill Islands, East Antarctica; development of a baseline for monitoring climate change impacts

J. Wasley[a*], S. A. Robinson[b], J. D. Turnbull[b], D. H. King[b], W. Wanek[c] and M. Popp[c]

[a]Terrestrial and Nearshore Ecosystems: Environmental Change and Conservation , Australian Antarctic Division, Kingston, Australia; [b] Institute for Conservation Biology and Environmental Management, University of Wollongong, Wollongong, Australia; [c] Faculty of Life Sciences, Department of Terrestrial Ecosystem Research, University of Vienna, Vienna, Austria

Abbreviations: ASPA: Antarctic Specially Protected Area, IRMS: isotope ratio mass spectrometry, N: nitrogen, TWC: turf water content.

* Corresponding author. Email: Jane.Wasley@aad.gov.au

Supplemental information available at:

http://data.aad.gov.au/aadc/portal/download_file.cfm?file_id=3595

Abstract

Extreme environmental conditions prevail on the Antarctic continent and limit plant diversity to cryptogamic communities, dominated by bryophytes and lichens. Even small abiotic shifts, associated with climate change, are likely to have pronounced impacts on these communities that currently exist at their physiological limit of survival. Changes to moisture availability, due to precipitation shifts or alterations to permanent snow reserves will most likely cause greatest impact. In order to establish a baseline for determining the effect of climate change on continental Antarctic terrestrial communities and to better understand bryophyte species distributions in relation to moisture in a floristically important Antarctic region, this study surveyed finescale bryophyte patterns and turf water and nutrient contents along community gradients in the Windmill Islands, East Antarctica. The survey found that the Antarctic endemic, *Schistidium antarctici*, dominated the wettest habitats, *Bryum pseudotriquetrum* distribution spanned the gradient, whilst *Ceratodon purpureus* and *Cephaloziella varians* were restricted to driest habitats. These patterns, along with knowledge of these species relative physiology, suggest the endemic *Schistidium antarctici* will be negatively impacted under a drying trend. This study provides a model for quantitative finescale analysis of bryophyte distributions in cryptogamic communities and forms an important reference site for monitoring impacts of climate change in Antarctica.

Keywords: water content; stable isotopes; soluble carbohydrates; moss; ∂13C; ∂15N

Introduction

Antarctic bryophytes are restricted to areas receiving reliable summer melt (Smith 1999) and nutrients may also affect distributions (Wasley et al. 2006a). Understanding current distributions and how they are influenced by these factors will inform climate change predictions for future vegetation dynamics (Robinson et al. 2003; Wasley et al. 2006a).

The Windmill Islands supports some of the most extensive and best-developed vegetation on continental Antarctica (Smith 1988); comprising at least 27 macrolichens and four bryophytes. The bryoflora is composed of three moss species (*Schistidium antarctici* (Cardot) L.I. Savicz & Smirnova (syn. *Grimmia antarctici* Card.); *Bryum pseudotriquetrum* (Hedw.) Gaertn., B. Mey. & Scherb. and *Ceratodon purpureus* (Hedw.) Brid) and one liverwort (*Cephaloziella varians* (Tayl.) Steph.).

Broadscale vegetation patterns in the Windmill Islands include a prevalence of moribund bryophyte turf encrusted with lichens; suggesting the lichen-dominated vegetation is expanding, and bryophyte communities are contracting to low-lying areas with reliable moisture supply. These dynamics are thought to be a response to regional uplift and climatic drying since deglaciation (Melick & Seppelt 1997) as well as more recent climate change (Clarke et al. 2012). The bryophyte-lichen community gradient that occurs in this region offers a model system to observe vegetation change in response to a changing environment. If regional drying persists, a continued expansion of moribund bryophytes and encrusting lichens into the present healthy bryophyte zone is expected. Alternatively, under a wetter climate, regeneration of moribund moss (demonstrated experimentally by Melick & Seppelt 1997) could lead to expansion of bryophyte communities.

Detecting future vegetation change requires a baseline for current distributions. The bryoflora is likely to be the most sensitive vegetation component to target for this purpose, as

growth rates (mean 0.6-1.3 mm y^{-1}; Clarke et al. 2012) are greater than that of lichens (<0.1 mm y^{-1}; Sancho et al. 2007), which are impractically slow. Whilst previous investigations of vegetation distributions in the Windmill Islands, have examined broadscale patterns (over meters to kilometres; e.g. Melick et al. 1994; Melick & Seppelt 1997; Smith 1988), patterns of individual species distributions within bryophyte communities are not well understood; current knowledge has been derived from a single transect (Selkirk & Seppelt 1987). This work indicates distributions may be determined by water availability and the present study uses quantitative finescale methods (over centimetres to meters) to confirm these patterns.

We also use stable isotope methodologies to assess water availability across the environmental gradient, as carbon isotopes are indicators of water history regime. More positive $\delta^{13}C$ values indicate less photosynthetic isotopic fractionation, reflecting diffusional limitations to CO_2. In cryptogams, which lack stomata, diffusional fractionation likely reflects the degree to which plants are submerged (Proctor et al. 1992; Rice & Giles 1996) and mosses subject to submergence may thus be expected to show more positive $\delta^{13}C$ signatures compared to those from drier habitats (Clarke et al. 2012).

Fractionation of nitrogen isotopes provides information about plant nitrogen sources. Antarctic plants commonly have high $\delta^{15}N$, due to utilisation of nutrients derived from marine sources (Cocks et al. 1998; Erskine et al. 1998; Robinson 2001; Lee et al. 2009). In many Antarctic sites, plants have colonised abandoned penguin rookeries (Hovenden & Seppelt 1995). Nutrients deposited when rookeries were occupied, between 2000 and 8000 years ago in the case of the Windmill Islands (Emslie & Woehler 2005; Goodwin 1993), undergo further ^{15}N fractionation as the guano passes through additional trophic levels associated with decomposition. Plants utilising this ancient nitrogen (N) source are expected to have exceptionally high $\delta^{15}N$ values (> +14.6‰, the value for fresh penguin guano).

Lower $\delta^{15}N$ values likely indicate plants are receiving a higher proportion of depleted N, such as volatilised wind-born NH_3 and/or fixing atmospheric N (Erskine et al. 1998).

In this study, we examined vegetation patterns, and their associated biochemical and environmental variables (turf water, plant nitrogen, carbon, $\delta^{15}N$, $\delta^{13}C$) along a series of transects that cross a community gradient extending from pure bryophyte stands to lichen-encrusted communities (described as Groups 1 to 2.2 in Melick & Seppelt 1997); forming a baseline for detecting future vegetation change and improving our understanding of water and nutrient relations in these floristically important Antarctic communities.

Methods

The study was conducted in the Windmill Islands, East Antarctica (described in Melick et al. 1994). Two sites, located in the north of the region were used (see Supplemental information, Figure S1): (1) Antarctic Specially Protected Area (ASPA) 135, on Bailey Peninsula (66.283°S, 110.533°E); and (2) Robinson Ridge (66.368°S, 110.587°E) designated ASPA2 and Robinson Ridge in Dunn & Robinson (2006).

Within the two sites 10 transects were established which spanned the bryophyte community gradient; from pure bryophyte stands, to the point at which the bryophyte turf was predominantly moribund and encrusted with lichens (lengths = ASPA: 1.4 -3.1 m, Robinson Ridge: 1.1-3.9 m). Three quadrat positions were established per transect: one at each end (referred to as: Bryophyte and Lichen communities) and the middle (referred to as: Transitional community). Each quadrat (20 x 20 cm) was divided into a 5 cm grid and a tweezer-pinch sample (approx. 20-50 gametophytes) collected at nine grid line intersections. Samples were stored air dried until analysis.

Samples were examined using a dissecting microscope. Bryophytes were categorised as moribund (brown) or healthy (green). Healthy bryophytes were identified to species level (*B.*

pseudotriquetrum, *S. antarctici*, *C. purpureus* or *C. varians*). Whilst the Windmill Islands region supports a rich lichen flora, the gradient examined here did not extend into lichen-dominated communities (see Melick & Seppelt 1997). Macrolichens, such as from the genera *Usnea*, *Umbilicaria* and *Pseudophebe*, occurred only in trace abundance (data not shown). Crustose lichens are presented as a combined group because identification to finer taxonomic level was not consistently possible across this group, especially given the small (tweezer-pinch) sample size. For each of the nine samples per quadrat, relative abundance was estimated for each species or taxonomic category via a modified Braun-Blanquet scale (Dominant=four, Co-dominant=three, Low abundance=two, Trace=one and Absent=zero). The sum of the nine relative abundance scores determined percent relative abundance for each quadrat; 100% represents dominant in all nine sub-samples.

Turf water content (TWC) was measured for each quadrat. Plant samples (2 cm diameter, up to 3 cm depth) were collected 17/2/00 (Robinson Ridge) and 28/2/00 (ASPA) in airtight vials, returned to the laboratory within 1 hour and processed as described in Robinson et al. (2000).

Background soil nitrogen and carbon were determined from six soil samples collected from within the bryophyte community at each of the two sites. Samples were analysed for %N, %C, $\delta^{15}N$ and $\delta^{13}C$, using isotope ratio mass spectrometry (IRMS). Plant %N and %C, stable isotopic signatures (δ15N & δ13C), and soluble carbohydrate contents (Supplemental information) were measured for plant community samples and thus integrate the response for the collection of species present. Species specific measurements were not possible because of the highly mixed nature of these cryptogamic communities (illustrated in Figure 1), as demonstrated by Stevens et al. (2007). Samples were measured by continuous-flow IRMS (Hietz et al. 1999), as described in Wasley et al. (2006a).

Two-way ANOVA tested site*community effects (sites: Robinson Ridge or ASPA and communities: Lichen, Transitional or Bryophyte). For soils 1-way ANOVA was used to test for site effect.

Results

Vegetation community

Transects were dominated by healthy bryophytes, with relative abundance exceeding 50% across all communities (Figure 2); highest in the Bryophyte community (> 90%) and declined to 50-60% in the Lichen community (community: $F_{36,2}$=12.0039, P = 0.0001). Moribund bryophytes, indicative of past healthy bryophyte presence, showed the inverse; highest abundance in Lichen community (> 50%) and lowest in Bryophyte community (< 10%; community: $F_{36,2}$=19.2332, P < 0.0001). Crustose lichen showed a similar trend; relative abundance > 40% in Lichen community and ~5% in Bryophyte community (community: $F_{36,2}$=25.6059, P < 0.0001).

Analysis at species level showed the Antarctic endemic, *S. antarctici*, as most abundant (max = 98% and >20% across all communities; Figure 3). This species was most abundant in the Bryophyte community (> 85%) but showed a 3-fold decline across the gradient (community: $F_{36,2}$=12.8896, P < 0.0001). In contrast, abundance of *C. purpureus* was greatest in the Lichen community (20-30%) and declined in the opposite direction to *S. antarctici* (community: $F_{36,2}$=14.1351, P < 0.0001). *Ceratodon purpureus* was absent from the Bryophyte community at both sites. These patterns were statistically similar between sites for *S. antarctici* and *C. purpureus*, but differed for *B. pseudotriquetrum* (site: $F_{36,1}$=5.2861, P = 0.0274). At Robinson Ridge, *B. pseudotriquetrum* abundance was consistently low (< 11%), while in the ASPA Lichen and Transitional communities abundance reached $\geq$30%. The

liverwort, *C. varians*, occurred only in low abundance (< 7%), and like *C. purpureus*, was absent from the Bryophyte community at both sites.

Plant and soil chemistry

Plant N and TWC correlated with the community gradient in opposing directions (community: $F_{54,2} = 8.152$, P = 0.001 and $F_{52,2} = 6.455$, P = 0.003, respectively; Figure 4). Bryophyte community turf had highest TWC, approaching 1.5 g H_2O g^{-1} dw, and lowest nitrogen concentrations, 1.6 % N, whilst the Lichen community was driest, 0.5-1.0 g H_2O g^{-1} dw with highest N contents (>2% N; Figure 3B). Percent carbon ranged from 50-61% and was similar across communities ($F_{50,2} = 1.607$, P = 0.211), but was approximately 10% lower at the ASPA site (range: 50-57%), compared to Robinson Ridge (range: 58-61%; site: $F_{50,1} = 13.325$, P<0.001).

A significant plant $\delta^{15}N$ gradient correlated with the community gradient, with values highest in the Bryophyte community (up to 20‰; Figure 4C). This pattern was observed at both sites, however, values for $\delta^{15}N$ were higher and the gradient steeper at the ASPA site (site*community: $F_{52,2} = 3.7406$, P = 0.0304). Lowest $\delta^{15}N$ values (less than 7‰) occurred in the Robinson Ridge Lichen community. The Bryophyte community had highest values for $\delta^{13}C$ (community: $F_{52,2} = 8.291$, P = 0.0007; Figure 4D), approximately 1‰ greater than the Lichen community signature.

Bryophyte community soil %N and %C was less than 0.1% and 1%, respectively, with no significant difference between sites (Table I). Soil %N was therefore very low compared to plant %N (c.f. Table I & Figure 4). The soil C/N was 20% lower at Robinson Ridge than at ASPA (P < 0.05; Table I). Stable isotope signatures for soil were slightly enriched compared to corresponding bryophyte material and followed the same site trends (c.f. Table I & Figure 4). Soil $\delta^{15}N$ was 9‰ lower at Robinson Ridge than at ASPA (P < 0.05; Table I) but soil $\delta^{13}C$ varied less than 1‰ between sites.

Discussion

Plant moisture and nutrient gradients operated in opposite directions across the community gradient, with TWC decreasing and plant nutrients increasing from the Bryophyte to the Lichen community. Elevated $\delta^{13}C$ values in the Bryophyte community indicate the Bryophyte community is subject to periodic submergence (Proctor et al. 1992; Rice & Giles 1996). Species-specific variation in $\delta^{13}C$ should be considered (Galimov 2000; Huiskes et al. 2006), but field observations and unpublished data (Robinson) support submergence as the driver of $\delta^{13}C$ patterns in these communities.

The wet, Bryophyte end of the transects were dominated by the Antarctic endemic, *S. antarctici*, with only trace levels of abundance detected for the cosmopolitan *B. pseudotriquetrum.* This pattern concurs with the results of the single ASPA transect surveyed by Selkirk & Seppelt (1987), however, in contrast to the previous study, *S. antarctici* was not simply restricted to wet areas, but was present across all three communities, albeit at low levels of abundance in the drier regions. Conversely, the other three bryophytes were absent from the wetter end of the gradient. *Bryum pseudotriquetrum* was the most evenly distributed species and this pattern is supported by its known physiological plasticity (Robinson et al. 2000, Wasley 2006b).

Healthy gametophytes, including *S. antarctici*, were detected (via microscopy methods) in moribund turf across the gradient; thereby documenting bryophyte occurrence in habitats that would be missed if relying on field survey techniques.

In contrast to Windmill Islands distributions, where *C. purpureus* and the liverwort *C. varians* are restricted to drier sites and *S. antarctici* dominates the wettest areas (Wasley et al. 2006b; Selkirk & Seppelt 1987), in the Ross Sea region *C. purpureus* has been reported as dominant in the wettest areas whilst *Bryum* species were more common in slightly drier areas

(Seppelt et al. 2010) and in the maritime Antarctic, *C. varians* was found in moist to wet environments (Newsham 2010) whilst *S. antarctici* is found in "dry" sites on Signy Island (Smith 1972). Comparisons of seasonal water availability (or $\delta^{13}C$ measurements) in bryophytes from these other sites would be useful to standardise and explain these contrasting results.

Whilst we propose here that species distributions are driven by water availability, it should also be considered that species-specific differences, with respect to water holding capacity, may play a role (Robinson et al. 2000; Gimingham 1967). We consider a species-driven scenario less likely for this continental Antarctic site however, as these bryophyte-dominated communities are restricted to areas of reliable free-water (as can be seen in Figure 1) and Robinson et al. 2000 demonstrates that each of these species increase water content by 3 to 4-fold in a wet compared to dry sites.

Species richness often increases with moisture availability (Turner et al. 2006; Treonis et al. 1999; Smith et al. 2010) however in this environment species richness peaked at intermediate water contents, where all four bryophyte species and a range of crustose lichens were supported. This trend is similar to that observed for the vegetation of Botany Bay in southern Victoria Land (Seppelt et al. 2010) and in other Windmills Islands studies (Melick & Seppelt 1997). This pattern has implications for diversity under a changing climate, and suggests that habitats supporting transitional zones will be important diversity refuges.

Whilst we have identified water availability as a key environmental driver for the composition of these communities, it should also be considered that other abiotic factors, such as nutrients (Wasley et al. 2006a) and biotic factors including inter-species associations (Upson et al. 2007) may also play a role in determining species distributions in these communities.

Nutrients from abandoned penguin colonies

Plant $\delta^{15}N$ was relatively high (>10‰ in Bryophyte community; c.f. Schulze et al. 1994; Miller & Bowman 2002). Elevated ^{15}N signatures are well documented in the Antarctic, due to a high proportion of animal-derived nutrients (e.g. seabird guano; 13.1 to 25.9‰; Cocks et al. 1998) and high rates of ammonium volatilisation; and our values are similarly enriched (Erskine et al. 1998; Bokhorst et al. 2007; Lee et al. 2009). As birds are not currently nesting within these sites (Supplemental information, Figure S1), the primary source is likely leached N from nearby ancient penguin rookeries abandoned many thousands of years ago (Emslie & Woehler 2005).

The ^{15}N gradient shows variation in nutrient source across the communities, as has been observed in maritime Antarctica (Bokhorst et al. 2007; Lee et al. 2009). The elevated $\delta^{15}N$ signatures found in the Bryophyte community (>15‰ for both plant and soil) indicate a predominant use of animal-derived N enriched, through repeated tropic transfer via microbial activity since guano deposition. Conversely, the Lichen communities lower $\delta^{15}N$ signatures indicate a reliance on N sources such as wind-born $\delta^{15}N$-depleted NH_3 from active penguin rookeries and atmospheric N deposited in snow (Bokhorst et al. 2007; Erskine et al. 1998; Lee et al. 2009; Zhu et al., 2009). As previously discussed with respect to variations in $\delta^{13}C$, whilst species-specific variation in $\delta^{15}N$ might play a role in the patterns observed (Bokhorst et al. 2007; Galimov 2000; Huiskes et al. 2006) it is more likely that N-source varies across these gradients. Despite these communities being separated by short distances (a few meters) the bryophyte community receives its nutrients from free water sources, whilst the lichen community is not exposed to free water and instead receives nutrient inputs from precipitation and windborne sources.

The plant nutrient gradient occurred in the opposite direction to water, with highest plant %N in the Lichen community. Although this could reflect compositional differences (lichens

have chitinous (fungal) cell walls which contain N) this is unlikely because the lichen contribution to biomass is small relative to the moss component (see Figure 1 & 2 and also Hovenden 2000). Although low %N in the Bryophyte community might indicate this community is more nutrient-limited than the other communities (see Wasley et al. 2006a), it more likely reveals a productivity gradient; moist bryophytes are more photosynthetically active, grow faster and therefore dilute their N reserves with carbon. High C/N ratios and high concentrations of soluble carbohydrate contents in the Bryophyte community (Wasley 2004; Supplemental information, Figure S2) support the presence of this productivity gradient. In contrast, low water contents are most likely limiting carbon fixation in the lichen community, leading to high %N and low C/N, as shown previously (Wasley et al. 2006a).

Predictions for future species dynamics

The community gradient investigated in this study, which covers the entire ecological range of past and present bryophyte occupation, is primarily determined by plant water availability. Pure bryophyte communities thrive in the wettest zones but are increasingly overgrown by crustose lichen-dominated communities in the drier areas. If conditions become wetter in future, healthy bryophytes are likely to increase in distribution and the presence of healthy material from all four bryophytes in moribund turf should support bryophyte regeneration and high species richness, as suggested in Wasley et al. (2006b). Additionally *S. antarctici* should be advantaged and expand the area it dominates whilst *Ceratodon purpureus,* which is intolerant of wetter habitats and is currently restricted to drier sites, might shift its distribution to habitats presently too dry for bryophyte occupation. *Bryum pseudotriquetrum*, which has a relatively broad and consistent distribution, appears to be least affected by changes in water content. Therefore regardless of climate shift direction, this species is likely to survive, but will not necessarily dominate future communities.

Under drier conditions, healthy bryophytes are likely to continue to retreat, further decreasing the extent of the bryophyte zone and increasing lichen dominance. The relatively desiccation tolerant, *C. purpureus* (Robinson et al. 2000; Wasley et al. 2006b) is most likely to survive a continuation of the present drying trend and might expand into areas which are currently too wet. Conservation of the endemic *S. antarctici* may become an issue if the current drying trend persists, since it is predicted to be most severely disadvantaged, as the habitats it dominates will recede and potentially disappear.

Acknowledgements

This research was supported by grant funding, permits and logistic support from the Australian Antarctic Science grants 1087 and 1313 and ARC Discovery project DP110101714. JW and DK would like to acknowledge funding from Australian Postgraduate Awards. We thank Andrew Netherwood for preparing Figure 1

References

Bokhorst, S., A.H.L. Huiskes, P. Convey and R. Aerts. 2007. Climate change effects on organic matter decomposition rates in ecosystems from the Maritime Antarctic and Falkland Islands. *Global Change Biology* 13: 2642-53.

Bokhorst, S., A. Huiskes, P. Convey and R. Aerts. 2007. External nutrient inputs into terrestrial ecosystems of the Falkland Islands and the Maritime Antarctic region. *Polar Biology* 30(10): 1315-1321.

Clarke, L.J., S.A. Robinson, Q. Hua, D.J. Ayre and D. Fink. 2012. Radiocarbon bomb spike reveals biological effects of Antarctic climate change. *Global Change Biology* 18: 301-10.

Cocks, M.P., D.A. Balfour and W.D. Stock. 1998. On the uptake of ornithogenic products by plants on the inland mountains of Dronning Maud Land, Antarctica, using stable isotopes. *Polar Biology* 20, 107-11.

Dunn, J.L. and S.A. Robinson. 2006. Ultraviolet B screening potential is higher in two cosmopolitan moss species than in a co-occurring Antarctic endemic moss: Implications of continuing ozone depletion. *Global Change Biology* 12: 2282-96.

Emslie, S. and E. Woehler. 2005. A 9000-year record of Adélie penguin occupation and diet in the Windmill Islands, East Antarctica. *Antarctic Science* 17: 57-66.

Erskine, P., D. Bergstrom, S. Schmidt, G. Stewart, C. Tweedie and J. Shaw. 1998. Subantarctic Macquarie Island - a model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance. *Oecologia* 117: 187-93.

Galimov, E. M. (2000). "Carbon isotope composition of Antarctic plants." *Geochimica Et Cosmochimica Acta* 64(10): 1737-1739.

Gimingham, C. H. 1967. Quantitative community analysis and Bryophyte ecology on Signy Island. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 252(777): 251-259.

Goodwin, I. 1993. Holocene deglaciation, sea level change, and the emergence of the Windmill Islands, Budd Coast, Antarctica. *Quaternary Research* 40: 70-80.

Hietz, P., W. Wanek and M. Popp. 1999. Stable isotopic composition of carbon and nitrogen and nitrogen content in vascular epiphytes along an altitudinal transect. *Plant, Cell and Environment* 22: 1435-43.

Hovenden, M. 2000. Seasonal trends in nitrogen status of Antarctic lichens. *Annals of Botany* 86: 717-21.

Hovenden, M.J. and R.D. Seppelt. 1995. Exposure and nutrients as delimiters of lichen communities in continental Antarctica. *Lichenologist* 27, 505-16.

Huiskes, A. H. L., H. T. S. Boschker, D. Lud and T. C. W. Moerdijk-Poortvliet. 2006. Stable isotope ratios as a tool for assessing changes in carbon and nutrient sources in antarctic terrestrial ecosystems. *Plant Ecology* 182(1-2): 79-86.

Lee, Y., L. Hs and H. Yoon. 2009. Carbon and nitrogen isotope composition of vegetation on King George Island, maritime Antarctic. *Polar Biology* 32: 1607-15.

Melick, D., M. Hovenden and R. Seppelt. 1994. Phytogeography of bryophyte and lichen vegetation in the Windmill Islands, Wilkes Land, continental Antarctica. *Vegetatio* 111: 71-87.

Melick, D. and R. Seppelt. 1997. Vegetation patterns in relation to climatic and endogenous changes in Wilkes Land, continental Antarctica. *Journal of Ecology* 85: 43-56.

Miller, A.E. and W.D. Bowman. 2002. Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: Do species partition by nitrogen form? *Oecologia* 130: 609-16.

Newsham, K.K. 2010. The biology and ecology of the liverwort *Cephaloziella varians* in Antarctica. *Antarctic Science* 22, 131-43.

Proctor, M.C.F., J.A. Raven and S.K. Rice. 1992. Stable carbon isotope discrimination measurements in *Sphagnum* and other bryophytes: Physiological and ecological implications. *Journal of Bryology* 17: 193-202.

Rice, S.K. and L. Giles. 1996. The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnum*. *Plant Cell and Environment* 19: 118-24.

Robinson, D. 2001. ∂^{15}N as an integrator of the nitrogen cycle. *Trends in Ecology and Evolution* 16, 153-62.

Robinson, S.A., J. Wasley, M. Popp and C.E. Lovelock. 2000. Desiccation tolerance of three moss species from continental Antarctica. *Australian Journal of Plant Physiology* 27, 379-88.

Robinson, S.A., J. Wasley and A.K. Tobin. 2003. Living on the edge - plants and global change in continental and maritime Antarctica. *Global Change Biology* 9, no. 12: 1681-717.

Sancho, L.G., T.G. Allan Green and A. Pintado. 2007. Slowest to fastest: Extreme range in lichen growth rates supports their use as an indicator of climate change in Antarctica. Flora - Morphology, Distribution, *Functional Ecology of Plants* 202, 667-73.

Schulze, E.-D., F.S.I. Chapin and G. Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. *Oecologia* 100: 406-12.

Selkirk, P.M. and R.D. Seppelt. 1987. Species distribution within a moss bed in greater Antarctica. *Symposia Biologia Hungarica* 35: 279-84.

Seppelt, R.D., R. Türk, A. Green, G. Moser, S. Pannewitz, L. Sancho and B. Schroeter. 2010. Lichen and moss communities of Botany Bay, Granite Harbour, Ross Sea, Antarctica. *Antarctic Science* 22: 691-702.

Smith, J.L., J.E. Barrett, G. Tusnády, L. Rejtö and S.C. Cary. 2010. Resolving environmental drivers of microbial community structure in Antarctic soils. *Antarctic Science* 22: 673-80.

Smith, R. I. L. 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. *British Antarctic Survey Scientific Reports* 68.

Smith, R.I.L. 1988. Classification and ordination of cryptogamic communities in Wilkes Land, Continental Antarctica. *Vegetatio* 76: 155-66.

Smith, R.I.L. 1999. Biological and environmental characteristics of three cosmopolitan mosses dominant in continental Antarctica. *Journal of Vegetation Science* 10: 231-42.

Stevens, M.I., S.A. Hunger, S.F.K. Hills and C.E.C. Gemmill. 2007. Phantom hitch-hikers mislead estimates of genetic variation in Antarctic mosses. *Plant Systematics and Evolution* 263: 191-201.

Treonis, A.M., D.H. Wall and R.A. Virginia. 1999. Invertebrate biodiversity in Antarctic Dry Valley soils and sediments. *Ecosystems* 2: 482-92.

Turner, P.a.M., J.B. Kirkpatrick and E.J. Pharo. 2006. Bryophyte relationships with environmental and structural variables in Tasmanian old-growth mixed eucalypt forest. *Australian Journal of Botany* 54: 239-47.

Wasley, J. 2004. The effect of climate change on Antarctic terrestrial flora. PhD, University of Wollongong.

Wasley, J., S.A. Robinson, C.E. Lovelock and M. Popp. 2006a. Climate change manipulations show Antarctic flora is more strongly affected by elevated nutrients than water. *Global Change Biology* 12: 1800-12.

Wasley, J., S.A. Robinson, C.E. Lovelock and M. Popp. 2006b. Some like it wet – an endemic Antarctic bryophyte likely to be threatened under climate change induced drying. *Functional Plant Biology* 33: 443-55.

Zhu, R., Y. Liu, E. Ma, J. Sun, H. Xu and L. Sun. 2009. Nutrient compositions and potential greenhouse gas production in penguin guano, ornithogenic soils and seal colony soils in coastal Antarctica. *Antarctic Science* 21: 427-38.

Upson, R., Read, D.J., Newsham, K.K. 2007. Widespread association between the ericoid mycorrhizal fungus *Rhizoscyphus ericae* and a leafy liverwort in the maritime and sub-Antarctic. *New Phytologist* 176: 460.

Figures

Figure 1: Schematic showing the Robinson Ridge site and representative quadrats from the three communities. The arrow indicates increasing water availability. The peak (left) above the quadrats was formerly the site of an ancient penguin colony that has supplied most of the nutrients for the site, whilst the peak to the right shows the location of Odbert Island where present colonies are located.

Figure 2: Percent abundance of three broad vegetation components: (A) moribund bryophytes, (B) healthy bryophytes and (C) crustose lichen for the three communities (Bryophyte, Transitional and Lichen) at two sites, ASPA135 and Robinson Ridge. Bars represent mean ± SE, n=7. Different letters indicate means that are significantly different at P=0.017.

Figure 3: Percent abundance for the four bryophyte species; (A) *S. antarctici*, (B) *B. pseudotriquetrum*, (C) *C. purpureus* and (D) *C. varians* for the three communities (Bryophyte, Transitional and Lichen) at two sites, ASPA135 and Robinson Ridge. Bars represent mean ± SE, n=7. Different letters indicate means that are significantly different at P=0.017.

Figure 4: Turf water content (A), plant % nitrogen (B) and stable isotopes; ∂^{15}N (C) and ∂^{13}C (D) for the three communities (Bryophyte, Transitional & Lichen) at two sites, ASPA135 & Robinson Ridge. Bars represent mean ± SE, n=10. Different letters indicate means that are significantly different at P=0.006.

Table I: Transect physical properties (aspect, length, rise & slope) and soil chemistry characteristics (%N, %C, N:C ratio, $\delta^{15}N$ & $\delta^{13}C$) sampled from within bryophyte communities at the two sites, ASPA and Robinson Ridge. Variables which are significantly different between sites are in bold font and indicated as: * = P<0.05 and ** = P <0.0001.

Variable	N	ASPA		Robinson Ridge	
		Mean	SE	Mean	SE
Aspect (º from North)	7	84	21	62	14
Length (m)	7	2.53	0.29	2.06	0.37
Rise (m)	7	0.14	0.04	0.22	0.04
Slope **	**7**	**0.05**	**0.01**	**0.11**	**0.02**
% Nitrogen	6	0.07	0.02	0.05	0.01
% Carbon	6	0.52	0.13	0.41	0.10
Ratio C:N *	**6**	**7.15**	**0.07**	**8.93**	**0.43**
$\delta^{15}N$ **	**6**	**23.84**	**1.18**	**14.56**	**0.52**
$\delta^{13}C$	6	-23.76	0.24	-24.74	0.57

Figure 1

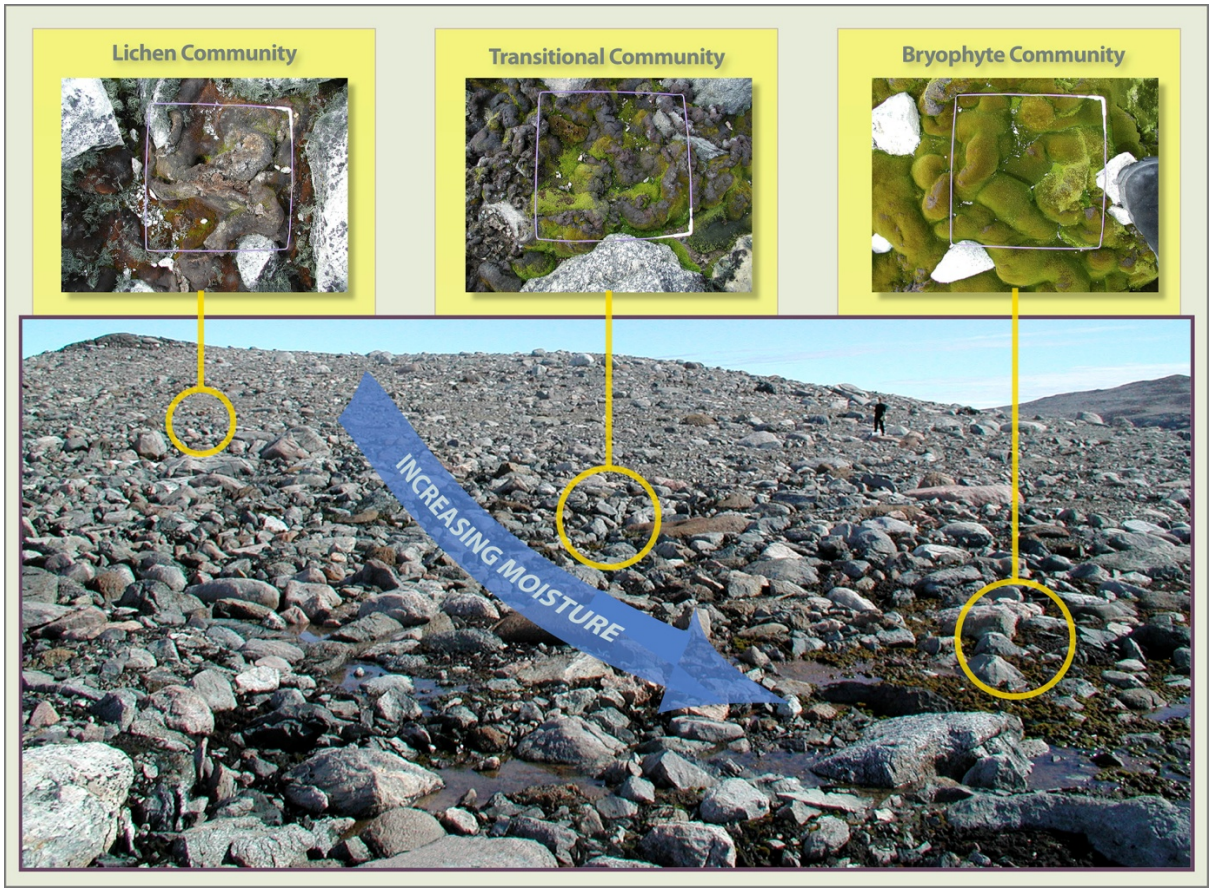

Lichen Community
Transitional Community
Bryophyte Community
INCREASING MOISTURE

Figure 2

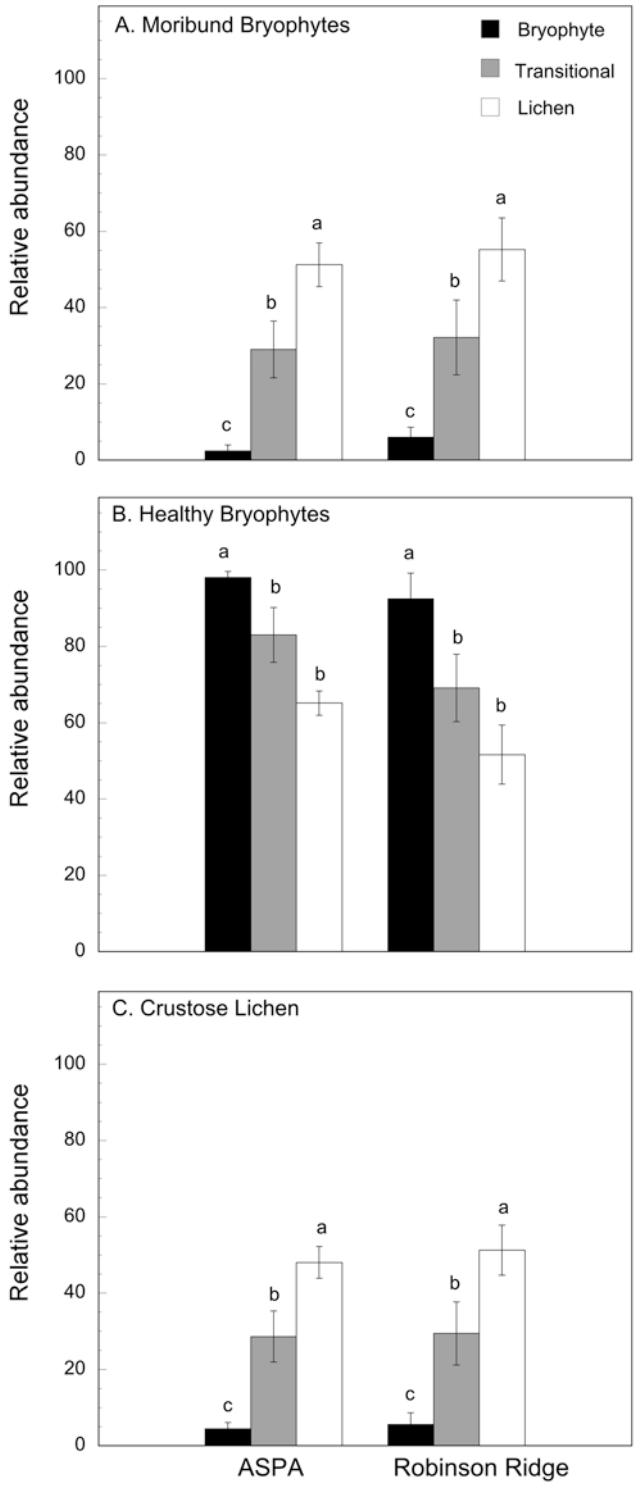

A. Moribund Bryophytes
Bryophyte
Transitional
Lichen
Relative abundance
100
80
60
40
20
0
c
b
a
c
b
a
B. Healthy Bryophytes
Relative abundance
100
80
60
40
20
0
a
b
b
a
b
b
C. Crustose Lichen
Relative abundance
100
80
60
40
20
0
c
b
a
c
b
a
ASPA
Robinson Ridge

Figure 3

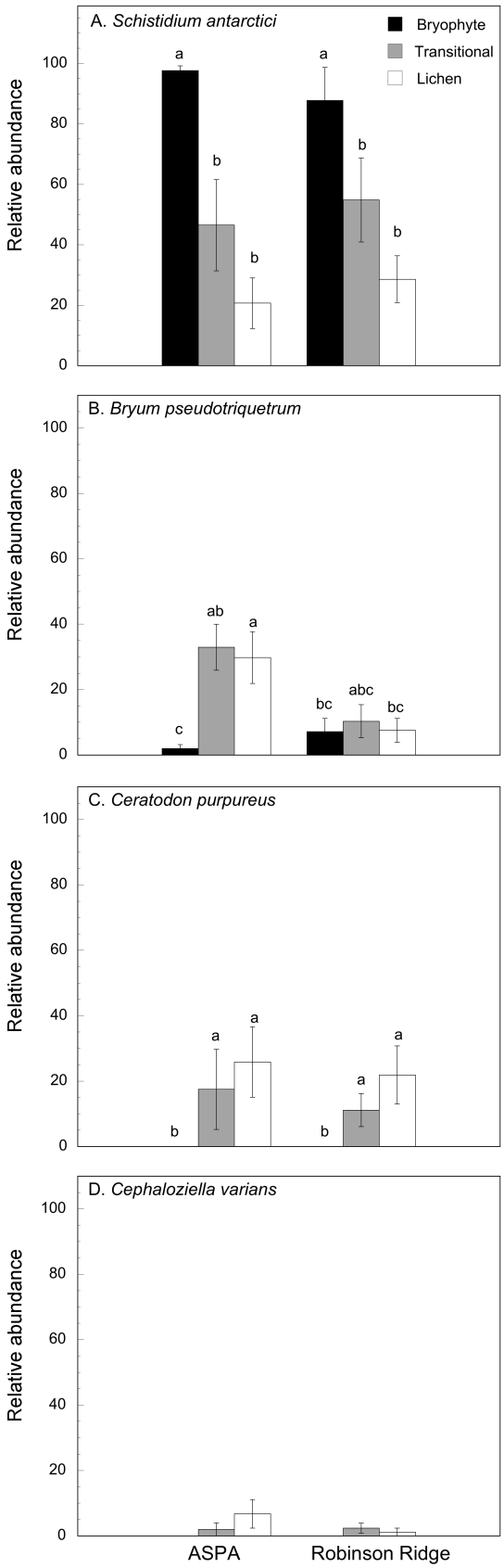
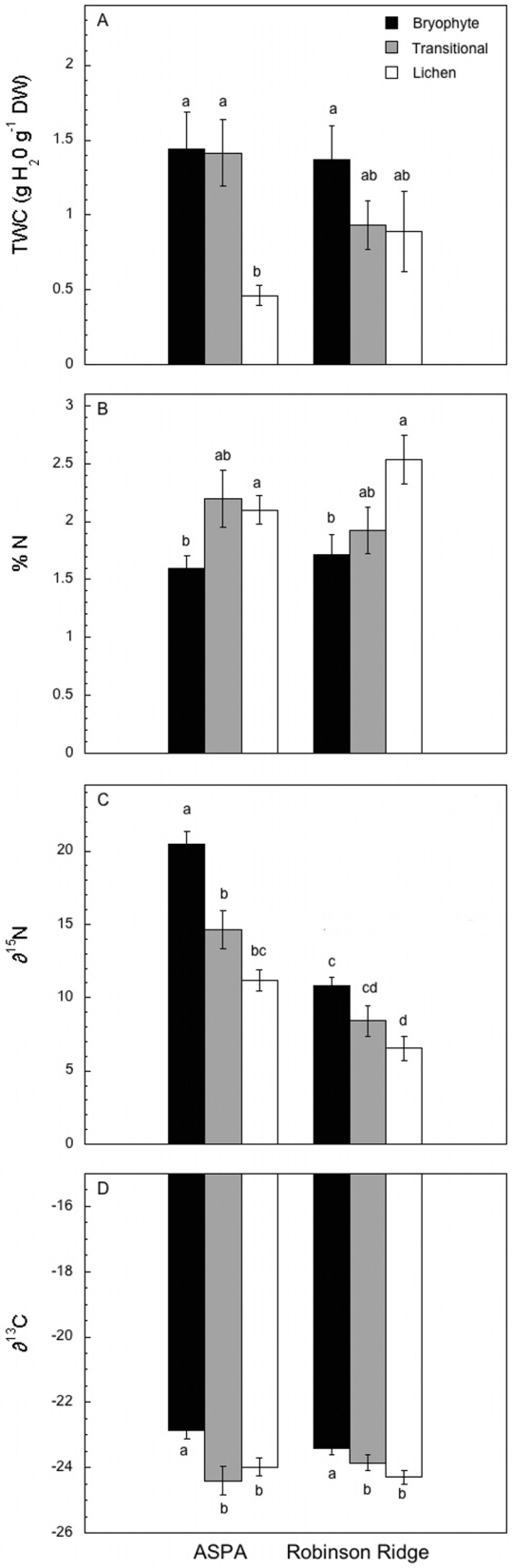

A. Schistidium antarctici
Bryophyte
Transitional
Lichen
Relative abundance
100
80
60
40
20
0
a
b
b
a
b
b
B. Bryum pseudotriquetrum
Relative abundance
c
ab
a
bc
abc
bc
C. Ceratodon purpureus
Relative abundance
b
a
a
b
a
a
D. Cephaloziella varians
Relative abundance
ASPA
Robinson Ridge

Figure 4


A
Bryophyte
Transitional
Lichen
TWC (g H2O g-1 DW)
B
% N
C
∂15N
D
∂13C
ASPA
Robinson Ridge

Supplemental information

Supplemental figure S1

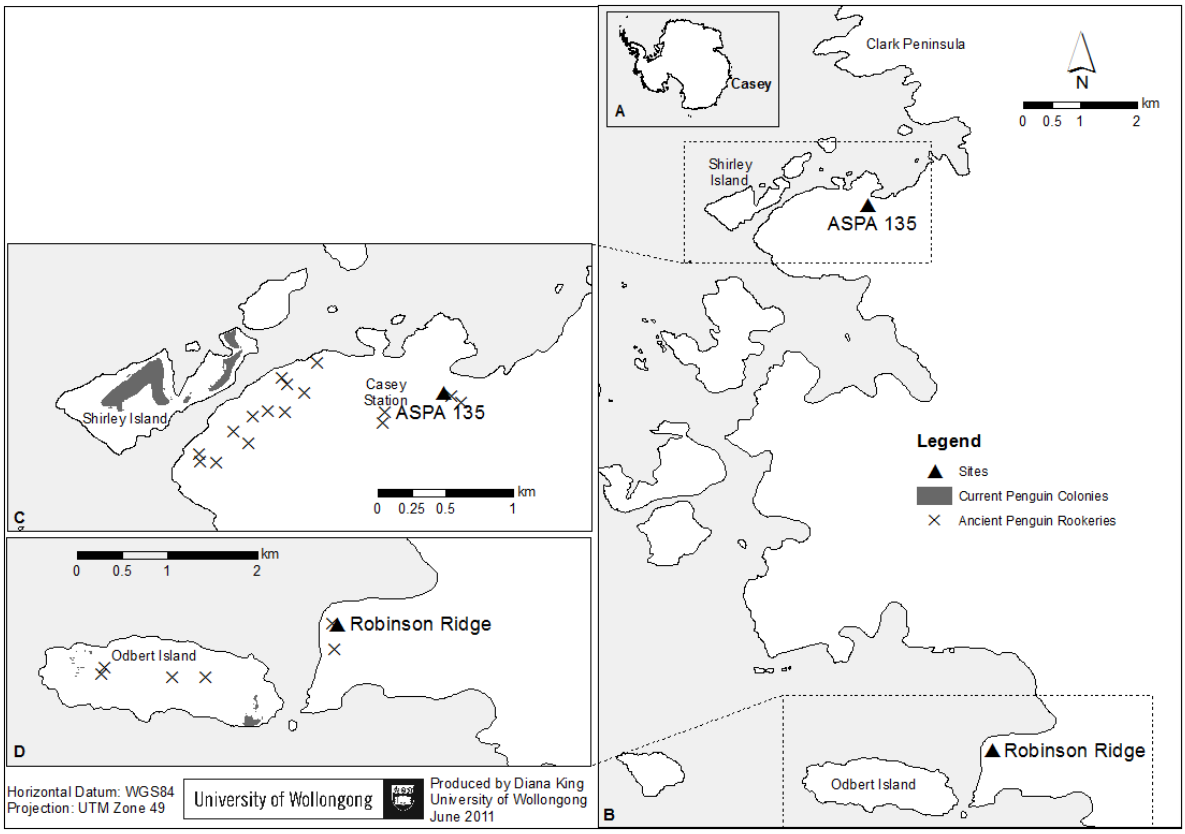


Figure S1: Map showing location of the Windmill Islands, East Antarctica (A,B), with location of study sites in detail, ASPA 135 (C) and Robinson Ridge (D). Locations of both ancient and current penguin colonies are also shown using data obtained from the Australian Antarctic Division Data Centre (AADC) Catalogue of Australian Antarctic and subantarctic Metadata (CAASM; http://data.aad.gov.au/aadc/metadata/; Goodwin & Harris (1999, updated 2007), Windmill Islands 1:10000 Some abandoned penguin colony site points; Harris, U. (1999, updated 2010) Windmill Islands 1:50000 Topographic GIS Dataset; Harris, U. and Woehler, E. (2001, updated 2006) Windmill Islands - Bird colonies 'eyed in' based on the field work of Eric Woehler and the GIS Dataset of Emslie & Woehler (2005).

Supplemental figure S2

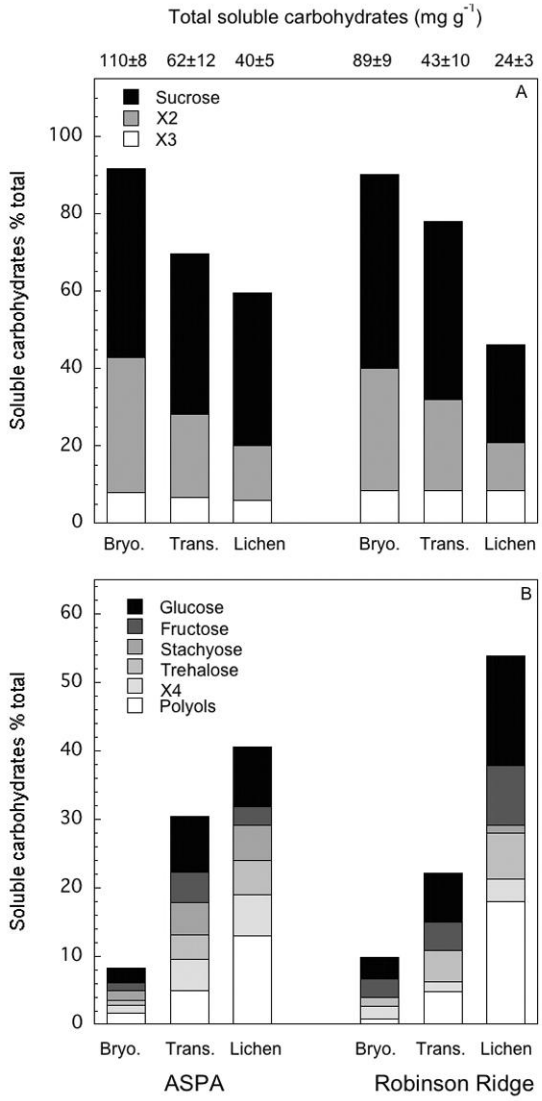


Figure S2: Plant soluble carbohydrate compositions for (A) major sugars (max. mean ≥ 5 mg g^{-1} dw); sucrose and unidentified X2 and X3 and (B) minor sugars (max. mean ≤ 4.9 mg g^{-1} dw); glucose, fructose, stachyose, trehalose, unidentified X4 and combined polyols (arabitol, glycerol, manitol, *myo*-inositol ribitol, sorbitol). Data represent means (n = 7) for the two sites, ASPA135 and Robinson Ridge and three community types: Bryophyte, Transitional and Lichen.

Plant soluble carbohydrate concentrations were determined for samples from each quadrat. Plant material was oven dried and ground (Wasley et al. 2006b) and soluble carbohydrates extracted in hot water and analysed using gas chromatography (as per Richter et al. 1990 and Wasley et al. 2006b).

Total soluble carbohydrate concentrations were almost 3-fold higher in the Bryophyte community than the Lichen community (community effect: $F_{54,2} = 31.6695$, $P < 0.0001$; Figure S2). The dominant sugars: sucrose and the unidentified X2 contributed most strongly to this pattern (Figure S2A). Several sugars important in cryoprotection and desiccation tolerance were detected (e.g. trehalose, stachyose and a range of sugar alcohols). These sugars made a significantly larger contribution to the soluble carbohydrate pool of samples from the Lichen community (25%) than the Bryophyte community (4%; Figure S2B).

Plant biochemical makeup varied along the community and resource gradient, with the Bryophyte community containing highest concentrations of total soluble carbohydrates, predominately sucrose and X2. Whilst mosses can accumulate sucrose in response to desiccation and freezing stresses (e.g. Nagao et al. 2005; 2006; Oldenhof et al. 2006), high concentrations of these sugars more likely reflect higher productivity in these wetter areas. Conversely, the drier, Lichen community contained the highest concentrations of several compounds likely to contribute toward increasing tolerance of desiccation, including trehalose and a range of sugar alcohols (mannitol, arabitol, ribitol and sorbitol; Smirnoff 1992, Roser et al. 1992). Under a drying climate we might expect to see a greater prevalence of these compounds, whilst more favourable growth conditions may result in an expansion of sucrose dominated plant carbohydrate content.

References

Nagao, M., Minami, A., Arakawa, K., Seizo Fujikawa, & Daisuke Takezawa. 2005. Rapid degradation of starch in chloroplasts and concomitant accumulation of soluble sugars associated with ABA-induced freezing tolerance in the moss *Physcomitrella patens*. *Journal of Plant Physiology*, 162, 169-180.

Nagao, M., Oku, K., Minami, A., Mizuno, K., Sakurai, M., Arakawa, K., Fujikawa, S., & Takezawa, D. 2006. Accumulation of theanderose in association with development of freezing tolerance in the moss *Physcomitrella patens*. *Phytochemistry,* 67(7), 702-709.

Oldenhof, H., Wolkers, W.F., Bowman, J.L., Tablin, F., & Crowe, J.H. 2006. Freezing and desiccation tolerance in the moss *Physcomitrella patens*: An *in situ* Fourier transform infrared spectroscopic study. *Biochimica et Biophysica Acta*, 1760, 1226-1234.

Richter A., Thonke B. & Popp M. 1990. ID-1-*O*-methyl-*muco*-inositol in *Viscum album* and members of the Rhizophoraceae. *Phytochemistry*, 29, 1785-1786.

Roser, D.J., Melick, D.R., Ling, H.U., & Seppelt, R.D. 1992. Polyol and sugar content of terrestrial plants from continental Antarctica. *Antarctic Science,* 4(4), 413-420.

Smirnoff, N. 1992. The carbohydrates of bryophytes in relation to desiccation tolerance. *Journal of Bryology*, 17, 185-191.